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THE HISTOLOGY OF THE PHLOEM IN CERTAIN WOODY ANGIOSPERMS[1]

L. H. MacDaniels

The study of phloem as a distinct tissue with an important and specialized function may be said to have begun in 1837, when Theodor Hartig discovered the sieve tube and announced that the sieve plates are perforated. This discovery, important as it was, apparently received little recognition for nearly twenty years, when Hartig's observations were confirmed and extended by Von Mohl (1855), Schacht (1860), Nägeli (1861), Hanstein (1865), and Dippel (1869). The work of these men, together with that of De Bary, established the fact of the universal occurrence of the sieve tube in the angiosperms, and of very similar structures in the gymnosperms and the vascular cryptogams.

The work of the last-named author is particularly significant in that, in addition to his own research, the work of previous investigators was brought together and organized and a nomenclature established which, for the most part, is still in use. Since the work of De Bary, numerous investigations on phloem have been published. From the physiological point of view the work of Fischer (1884), Haberlandt (1884), Czapek (1897), and others stands out as important; from the standpoint of histology, probably the most significant publications are those of Wilhelm (1880), Janczewski (1882), Russow (1883), Lecomte (1889), Poirault (1893), Perrot (1899), Strasburger (1901), and two papers by A. W. Hill (1901, 1908). These papers vary much in nature, but are concerned chiefly with the development and structure of the phloem of mature stems. The idea of relating anatomy and histology to taxonomy and phylogeny by the methods followed by Schwendener and Solereder, and, in a broader and more fundamental way, by Williamson and other workers in paleobotany, had not been applied to the phloem by any of these investigators. The papers of Jeffrey, however, in 1900 (11) and 1902 (12), laid renewed emphasis on the value of anatomy in taxonomy, maintaining that internal morphology should be given weighty consideration in working out phylogenetic relationships. Thus, mainly upon anatomical characters, the division of vascular plants into two great groups, the Lycopsida and the Pteropsida, has been made. In these papers Jeffrey has also put forth and strongly emphasized the importance in plants of the principle of recapitulation based on the fact that the seedling in its ontogeny often recapitulates ancestral characters. Hence, by the study of sporelings of pteridophytes and seedlings of angiosperms, stelar types in these groups and the probable evolution of the stele have been determined.

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[1] Contribution from the Department of Botany, College of Agriculture, Cornell University.

In addition to types of stele, various other characters have also been given weight in classification. Among these may be mentioned types of vessel and the distribution of parenchyma in xylem. It is held by the last-named author and others (6) that vessels with scalariform end walls are primitive, whereas those with porous ends are advanced. In the same way, the terminal position of the wood parenchyma is considered most primitive, the vasicentric position most advanced, and the diffuse position intermediate (9).

Phylogenetic significance was first assigned to types of sieve tubes found in angiosperms by A. F. Hemenway in two papers entitled "Studies on the Phloem of the Dicotyledons" (1911, 1913). In the first of these, covering six species of the Juglandaceae, the point is made that the sieve tubes of that family have well-developed sieve plates upon the side walls which do not differ from those on the end walls. Such a condition resembles that found in the gymnosperms and vascular cryptogams; hence the phloem of the Juglandaceae is primitive, and its sieve tubes represent the type primitive among angiosperms.

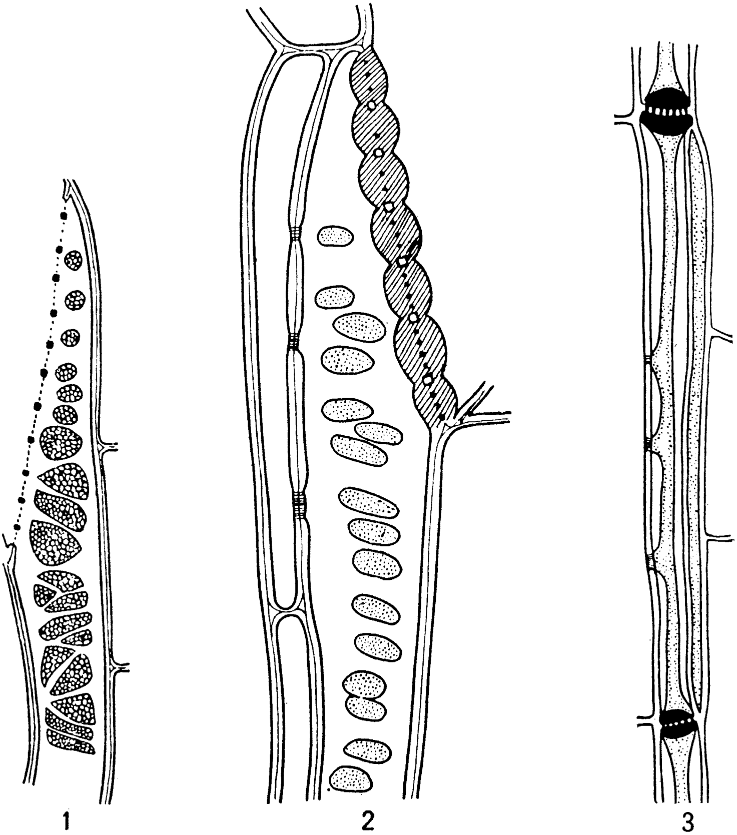
In Hemenway's second paper, after the study of ninety-six species of woody dicotyledons belonging to seventy-five genera and enough herbaceous monocotyledons and dicotyledons to make the total number of genera studied one hundred and forty, the following points are made:

The forms studied are grouped under three principal types which are indicated in text-figures 1–3, after Hemenway's figures.

The first type, according to that author, resembles the sieve tube of Pinus, with the sieve plates on the side wall identical with those on the end wall. The terminal wall in this case is very oblique, extending from one fourth to one half the length of the sieve tube element.

This type is shown in text-figure 1, representing the sieve tube of *Juglans nigra*.

"The second type is like the first except that the lateral sieve plates are less well developed and the end walls less oblique, having two to ten sieve plates each. This type may be shown by Vitis" (text-fig. 2). The sieve plates are shown covered with callus.



TEXT-FIGS. 1–3. Sieve tube segments are shown cut longitudinally in the tangential plane so that the sieve plates on the end walls are seen in section and those on the side walls are seen face view. (See text.)

The third type has the end wall made up of a single sieve plate which is placed nearly at right angles to the side walls. The sieve plates, or lattices, on the side walls are not so well developed as in the other types. This condition is illustrated by *Lactuca scariola* (text-fig. 3).

In these three types there is a correlation between the type of side wall and the type of end wall; type 1 has well-developed lateral plates, whereas type 3, the highest type, has the lattices poorly developed.

Thirty species of the lower woody dicotyledons were studied and found to have the same general sieve tube structure as have the gymnosperms and vascular cryptogams. In general there is no wide variation in type of sieve tube even in different genera of the same family, except when there are both herbaceous and woody genera within the family, in which case the herbaceous plants show the higher type.

No woody dicotyledons studied have sieve tubes of the third type. In the list of species arranged in groups according to type, the woody dicotyledons are placed almost exactly in the phylogenetic order of the Engler and Prantl system. The herbaceous dicotyledons and the monocotyledons are all placed above the second type.

Companion cells are rare if not wanting in many of the lower dicotyledons.

The evolution of the sieve tube parallels that of the vessel, there being a gradual transition from the gymnosperm type with oblique end walls and well developed lateral sieve plates to the so-called dicotyledonous type with transverse sieve plates and poorly developed plates or lattices upon the side walls.

The study of sieve tube types adds an argument in favor of the view that herbaceous plants are more advanced in evolutionary development than woody plants.

The initial purpose of the present research was to make a study of the phloem of seedlings of a number of woody dicotyledons selected to represent a series from those phylogenetically lowest to those highest in the Engler system. Such a study was expected to reveal any differences between the structure of the phloem in the seedling and in the mature plant, both root and stem, and to supply evidence of recapitulation. If the latter were present, it was hoped that light would be thrown on what constitutes the primitive type of sieve tube among angiosperms. As the work progressed, however, discrepancies of a rather startling nature began to appear between the results of the present research and those of Hemenway. Further, examination of literature showed that there are also many published descriptions of sieve tubes of woody dicotyledons which do not agree with Hemenway's classification. This led, in so far as time has allowed, to a checking of Hemenway's results in the woody dicotyledons by the careful examination of many of the species described by him. This has been taken up in addition to the seedling study originally planned.

The following material has been examined. Collections marked N. S. followed by the age, indicate material taken from a branch of that age on a mature tree. Mature phloem with few exceptions was taken during the dormant season from thrifty trees ten inches or more in diameter. Growing material was also taken from mature trees. Mature root material was obtained from the larger roots of mature trees.

List of Material Studied

Acer Negundo L.
Mature, twig.

Acer rubrum L.
Growing, twig.

Acer saccharum Marsh.
Mature, growing, mature root, 5-yr. stem, 1-yr. stem.

Aesculus Hippocastanum L.
Mature, twig.

Ailanthus glandulosa Desf.
Mature, N. S. 5-yr., mature root, growing, 5-yr. stem, 5-yr. root, 1- to 2-yr. stem, twig.

Alnus incana (L.) Moench.
Mature.

Benzoin aestivale (L.) Nees.
Mature, twig.

Betula lutea Michx. f.
Mature root, mature, 3-yr. stem, twig.

Carya cordiformis (Wang.) K. Koch.
Mature, 3-yr. stem.

Carya glabra (Mill.) Spach.
Mature root, 4-yr. stem, 3-yr. root, twig.

Carya ovata (Mill.) K. Koch.
1-yr. stem, 1-yr. root.

Castanea dentata (Marsh.) Borkh.
Mature.

Catalpa bignonioides Walt.
Mature, twig.

Celtis occidentalis L.
Mature.

Cephalanthus occidentalis L.
Mature, mature root, growing, 2-yr. stem, 4-yr. root, twig.

Cornus alternifolia L. f.
Mature.

Cornus Amomum Mill.
2-yr. stem, 2-yr. root.

Cornus paniculata L'Her.
Mature root.

Eleagnus angustifolia Pursh.
Growing.

Fagus grandifolia Ehrh.
Mature, twig.

Fraxinus americana L.
Mature, mature root, growing, 6-yr. stem, 6-yr. root, 2-yr. stem, 2-yr. root, 1-yr. twig.

Fraxinus nigra Marsh.
Mature, twig.

Gleditsia triacanthos L.
Mature.

Gymnocladus dioica (L.) Koch.
Twig.

Juglans cinerea L.
Mature, growing, mature root, 1-yr. stem, 1-yr. root, twig.

Juglans nigra L.
Mature, N. S. 10, 8, 6, 4, 2-yr., 4-yr. stem, 4-yr. root, 2-yr. stem, 2-yr. root.

Liriodendron Tulipifera L.
Mature, mature root, 10- to 12-yr. stem, 10- to 12-yr. root, 3-yr. stem, 3- to 4-yr. root, 3-yr. root, twig.

Maclura pomifera (Raf.) Schneider.
Mature.

Magnolia acuminata L.
Mature, mature root, 12-yr. stem, 5- to 7-yr. root, sucker shoot, 2-yr. twig.

Morus alba L.
Twig, mature.

Nyssa sylvatica Marsh.
Mature, twig.
Ostrya virginiana (Mill.) K. Koch.
Mature.
Platanus occidentalis L.
Mature stem, mature root, growing, 4-yr. stem, 4-yr. root, 2-yr. stem, 2-yr. root, twig.
Populus deltoides Marsh.
Mature, mature root, growing, 4-yr. stem, 4-yr. root, 3-yr. stem, 3-yr. root, 1-yr. stem, 1-yr. root.
Prunus Persica (L.) Stokes.
Mature.
Prunus serotina Ehrh.
Mature.
Pyrus communis L.
Mature.
Pyrus Malus L.
Mature old tree, mature young tree, growing, mature root, 5-yr. stem, 5-yr. root, twig.
Quercus alba L.
Mature, mature root, growing.
Quercus bicolor Willd.
Twig.
Quercus rubra L.
3-yr. stem, 3-yr. root.
Rhamnus alnifolia L'Her.
Twig.
Rhus typhina L.
Mature, growing, mature root, 3-yr. stem, 3-yr. root, 1-yr. stem, 1-yr. root, twig.
Ribes americana Mill.
2-yr. twig.
Robinia Pseudo-Acacia L.
Mature, growing, mature root, 4-yr. stem, 4-yr. root, 2-yr. stem, 2-yr. root, 1-yr. stem, 1-yr. root, twig.
Salix alba var. *vitellina* (L.) Koch.
Mature.
Salix nigra Marsh.
Mature, growing, mature root, 2-yr. stem, 2-yr. root.
Sambucus canadensis L.
Mature, growing, mature root, 3-yr. root.
Sambucus racemosa L.
1-yr. stem, 1-yr. root, twig.
Sassafras variifolium (Salisb.) Kuntze.
Root of small tree, 2-yr. twig.
Tilia americana L.
Mature, 3-yr. stem, 3-yr. root, 2-yr. stem, 2-yr. root, 1-yr. root, twig.
Ulmus americana L.
Mature stem, mature root, growing, 5- to 6-yr. stem, 5- to 6-yr. root, 3-yr. stem, 3-yr. root.
Ulmus fulva Michx.
Mature.
Viburnum Lentago L.
Mature, growing, mature root, 6- to 10-yr. root.

METHODS

A saw and a chisel were used in obtaining material from the trees. This was cut into approximately one-centimeter cubes including phloem and contiguous cambium and xylem, and killed in chrom-acetic acid, 0.75 percent–1 percent. It was then desilicified by placing it in hydrofluoric acid, one half commercial strength, for two weeks; dehydrated through a series of alcohols; embedded in celloidin; sectioned on a sliding microtome; stained in Delafield's haematoxylin and safranin, and mounted in balsam. It was found that collections made in the early fall soon after cambial growth stopped were usually in better shape than those made in the early spring before development began, because in many species the sieve tubes were badly crushed at the latter time.

The description of material is taken up in phylogenetic order. For the sake of brevity, many of the descriptions are omitted and the descriptions themselves are abridged. For convenience, the following outline is followed for the description of each species.

Sieve tubes:[2] Size; abundance; distribution; type of end wall—*i. e.*, type 1, very oblique with 10–20 sieve plates separated by scalariform bars; type 2, with oblique end wall with 2–10 sieve plates between scalariform bars; and type 3, with a single plate, either transverse or slightly oblique; lattice-description (by lattice is meant the sieve fields on the side walls of the sieve tubes).

Companion cells: abundance; distribution.

Parenchyma: distribution; abundance; type, whether "cambiform" (*i. e.*, elongated), prosenchymatous, or "conducting" (*i. e*, shorter, larger in diameter, and thin-walled, usually in series vertically. These terms are after Haberlandt, 4).

Salix nigra

Mature. Sieve tubes abundant, in irregular tangential rows between bands of fibers, not collapsed even in older portions; end walls oblique, of first type, with 8–15 sieve plates; lattice with fine pores between cellulose bands, almost identical with that of *Populus deltoides* (fig. 7); pores in sieve plates 2–3 μ in diameter, those in sieve fields of lattice about 0.4–0.5 μ.

Companion cells in the corners of about one third the sieve tubes, sometimes extending the entire width.

Parenchyma of one type, the divided cambiform; for the most part filled with dark-staining granules; heavily pitted on end and radial walls with sieve-like pits; cells about equal to sieve tubes in number; in tangential bands along the bands of fibers and scattered among the sieve tubes.

Growing. No new features except that fewer parenchyma cells are filled with tannin[3] in the current year's growth.

Mature root. Differs from mature stem only in having somewhat less sclerenchyma (fig. 8).

Two-year stem from rapidly growing plant. Sieve tubes few in number and small as compared with mature conditions; most elements with oblique end walls, a few with transverse sieve plates; on oblique end walls the plates are more widely separated than in mature phloem; lattice not well developed; walls of tubes apparently much thinner than in mature sieve tubes; actual breadth of sieve plates 10–20 μ as contrasted with 20–50 μ in mature.

Companion cells present in normal numbers.

Parenchyma of same type as mature.

Populus deltoides

Mature stem. Phloem identical with that of *Salix nigra* except in minor details. Smaller proportion of parenchyma filled with dark-staining granules than in Salix.

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[2] Although in its best usage the term sieve tube refers to a series of cells joined end to end (see De Bary, 2), for convenience the term is here also used to designate a single element or cell unit of a sieve tube.

[3] In this paper the term *tannin* is used to signify the dark brown cell content that is abundant in many plants. In many cases it is chemically tannin, but in others it is organic material of similar appearance.

Width of sieve plates 30–45 μ. Width of sieve pores 3.5–5.5 μ (fig. 2). Pores on side walls mere dots not over 0.5–0.6 μ, not so distinct and clear cut as in sieve plate (fig. 3).

Mature growing and *mature root* show no new features in phloem except reduction of sclerenchyma in latter (fig. 7).

Four-year stem. Rapid growth (fig. 6). Sieve tubes abundant, same type as mature but smaller, width of sieve plates 15–25 μ; plates not so crowded on terminal wall as in mature; lattice not well developed.

Companion cells in normal numbers.

Parenchyma abundant, of two types: one short, wide, usually filled with tannin, the other elongate, heavily pitted on the radial walls and not containing tannin.

Four-year root. Same as four-year stem except for increase in storage tissue and reduction of amount of sclerenchyma; all parenchyma full of starch.

Three-year stem. Slow growth (fig. 5). Same general features as in four-year stem but number and size of sieve tubes greatly reduced; lattice not well developed; width of sieve plates 12–20 μ.

Companion cells present.

Tissue packed with starch; length of sieve tubes less than in mature.

Three-year root. Sieve tubes smaller and fewer than in stem of same age. Pores on sieve plates not well developed; lattice not well developed, none observed; storage tissue abundant, packed with starch. Fewer sieve plates on end wall than in older material.

One-year stem (fig. 4). Sieve tubes very small and scarce, much more so than in the three-year material, difficult to find; some sieve plates transverse, usually only two or three plates on oblique walls. Width of sieve plates 6–10 μ; parenchyma full of starch.

One-year root. Same in general as one-year stem. Sieve tubes fewer in proportion to parenchyma; some with transverse walls in same section with those with as many as six sieve plates on an oblique end wall.

Juglans nigra

Mature (fig. 15). Phloem very much like that of Salix and Populus in general features. Sieve tubes abundant, scattered among parenchyma, of lowest type, with very oblique end walls, sometimes having as many as 20 sieve plates; lattice well developed, much as in Carya (fig. 9) but not so regular; pores visible but not more than 0.5–0.6 μ in diameter; pores on sieve plates 1.8 to 3.5 μ, as in Populus (figs. 2, 3).

Companion cells not abundant, probably present in about one sieve tube out of ten.

Parenchyma of divided cambiform type, frequently filled with dark staining substance.

N.S. 12 to N.S. 2. Phloem taken from the top at points at 12, 10, 8, 6, 4, and 2 years of age showed gradual decrease in size of sieve plate from 25–40 μ in width to 12–20 μ in the two-year material; also a reduction in number of sieve tubes as compared with the number of parenchyma cells, a reduction very similar to that observed in a series of seedlings of different ages.

Four-year stem (fig. 14). Sieve tubes small, 6–18 μ; few in proportion to parenchyma cells; lattice not well developed.

Companion cells rare, about as abundant as in mature.

Parenchyma of divided cambiform type; some cells longer than others.

Four-year root. Same as the four-year stem except more storage tissue; sieve tubes in groups separated by wide rays.

Two-year stem (fig. 13). Shows further reduction in size and number of sieve tubes and increase in proportional amount of parenchyma.

Two-year root. Same as the two-year stem except for increased amount of storage tissue.

Juglans cinerea

Mature, growing and *mature root* same as *Juglans nigra* except that latter has more fibers in phloem.

One-year stem (fig. 12). Sieve tubes very small and scarce; sieve plates 8–12 μ in width; lattice not apparent; oblique end wall with several plates with poorly developed pores; companion cells not found but probably present; parenchyma abundant, some cells elongated and conspicuously pitted, others short and packed with starch.

Carya cordiformis

Mature (fig. 9). Sieve tubes single or in groups of 3 or 4 surrounded by single row of parenchyma cells, each strand of sieve tubes and parenchyma embedded in an almost solid mass of fibers; sieve tubes with very oblique end wall, with 10 to 20 sieve plates (fig. 9); lattice very regular, cross-bars separating sieve fields; pores of sieve fields very minute, pores in sieve plates on end walls 3–4.5 μ in diameter.

Companion cells present in corners of sieve tubes, difficult to determine.

Parenchyma of divided cambiform type, abundantly pitted on radial walls, confined to sieve tubes or in narrow tangential bands; many cells filled with tannin.

Carya ovata

One-year stem, one-year root. Same as above-described species in essential features; sieve tubes small; 3 to 4 sieve plates on oblique end walls, plates rather widely separated; lattice very faint.

Companion cells probably present.

Parenchyma heavily pitted and abundant.

Fagus grandifolia

Mature. Sieve tubes large with single transverse sieve plates 50–60 μ across; pores on sieve plates large, 6–9 μ in diameter, pores on lattice distinct but small, about 0.5 μ; lattice not well developed.

Companion cells not easily seen on account of condition of material.

Parenchyma scattered, not abundant.

Castanea dentata

Mature. Sieve tubes in rather small numbers as compared with parenchyma; end walls oblique with 4–8 large sieve plates; lattice about as in Populus.

Companion cells rare.

Parenchyma of two types, one with protoplasmic contents, sometimes tannin, the other brick-shaped, apparently empty, with conspicuous sieve-like pitting on all walls especially the radial and terminal. (This type distinct and unusual.)

Ulmus americana

Mature (figs. 16, 17). Sieve tubes collapsed except close to cambium; sieve plates transverse with large meshes, 4–7 μ in diameter; lattice with prominent cross-bars and conspicuous pores (fig. 17); pores of lattice about 0.6–0.8 μ in diameter.

Companion cells frequent.

Parenchyma of two types: one large and tannin-filled, arranged in tangential rows; the other divided-cambiform, heavily pitted on radial walls, scattered among the sieve tubes.

Growing. No new features except reduction in amount of sclerenchyma.

Five- to six-year stem. Sieve tubes very small and scarce; of the same type as those of the mature stem; lattice not well developed.

Parenchyma as in mature but a proportionally larger amount in relation to sieve tubes.

Three-year root. Sieve tubes very rare, difficult to find; sieve plates transverse as in mature, but poorly developed; sieve tubes of about the size of some of the parenchyma cells.

Parenchyma abundant, thin-walled.

Maclura pomifera

Mature (fig. 18). Sieve tubes short and broad with transverse sieve plates in tangential bands between bands of heavily pitted parenchyma; lattice not well developed.

Companion cells fairly common.

Parenchyma of two types; one heavily pitted on radial and transverse walls, the other thin-walled, containing crystals; these arranged in bands in the following succession: 4–5 rows of heavily pitted parenchyma, 1–2 rows of crystal-containing parenchyma, 2–4 rows of sieve tubes.

Morus alba

Mature (fig. 19). Sieve tubes abundant, short, rather wide, with a single transverse sieve plate; lattice forming a distinct network as in Ulmus; pores in lattice distinct.

Companion cells in about one half of sieve tubes.

Parenchyma of divided cambiform type, heavily pitted on radial wall; not filled with tannin; scattered among sieve tubes and in irregular tangential bands.

Liriodendron Tulipifera

Mature (fig. 21). Sieve tubes of type 2, with 6–10 sieve plates upon an oblique end wall; lattice of rounded, well-defined sieve areas on both tangential and radial walls, most abundant on radial; side walls of younger tubes completely covered with a layer of bluish-staining substance, probably callus. Companion cells abundant in the corners and across the sides of the tubes.

Parenchyma not abundant; of divided-cambiform type, heavily pitted among the radial walls.

Mature root (figs. 22–25). Differs from mature stem only in having less sclerenchyma.

Three-year stem. Phloem areas small, between large fan-shaped rays. Sieve tubes small and few as compared with amount of parenchyma; sieve plates transverse in majority of cases; lattice not apparent.

Parenchyma of two types, the elongate phloem parenchyma distinct from the storage type.

Three-year root. Differs from stem of same age only in having no fibers and in having smaller amount of phloem as compared with storage tissue.

Twig. Sieve tubes small with sieve plates either on an oblique end wall or along sides of tubes.

Parenchyma of same type as in mature.

Sassafras variifolium

Root of small tree. Sieve tubes not abundant; single sieve plates transverse or. slightly oblique; lattice not well developed.

Companion cells not observed on account of collapsed condition of sieve tubes

Parenchyma of divided-cambiform type; heavily pitted upon radial walls.

Benzoin aestivale

Mature. Sieve tubes small, nearly occluded with callus-like substance; sieve plates single, either transverse or oblique; lattice not conspicuous.

Companion cells present in about one half of the sieve tubes.

Parenchyma of divided-cambiform type, partially filled with tannin-like substance; frequent large secretory cells.

Platanus occidentalis

Mature. Sieve tubes crushed except next cambium; large with oblique end walls; type 2, with 3–10 large plates 35–45 μ wide, frequently separated rather widely; lattice in the form of small pore areas upon both radial and tangential walls; no well-defined cross bars as in Populus.

Companion cells present in about one third of sieve tubes.

Parenchyma of divided-cambiform type, frequently filled with tannin; heavily pitted on the radial, and to some extent on the tangential walls.

Four-year stem. Phloem small in amount, in restricted areas between rays; sieve tubes small with transverse end plates, or plates upon side wall; plates small, 8–12 μ in width; lattice not apparent on uniformly thin side walls.

Four-year root. Like stem of same age.

Two-year stem. Sieve tubes showing sieve plates widely separated upon side walls; width of plates 6–8 μ.

Parenchyma elongated with abundant pitting.

Two-year root. Like stem of same age.

Pyrus Malus

Mature (*old tree*). Sieve tubes abundant, long and narrow with no clearly defined end wall (fig. 27); radial walls covered with closely set sieve plates sometimes in two rows (fig. 26); plates of different sizes; pores in different plates of nearly the same size, 0.8–1.5 μ, only a few with smaller pores; no sieve plates on the tangential walls.

Companion cells in about one half the sieve tubes.

Parenchyma of two types: one, the elongate-cambiform with well-developed protoplasts; the other longer, containing abundant crystals.

Prunus Persica

Mature (fig. 28). Sieve tubes next cambium filled with a blue-staining callus-like substance as in Benzoin, very narrow with end walls usually as in type 3; occasional end walls with more than one plate, but this exceptional; lattice not observed.

Companion cells not discernible with certainty.

Parenchyma of slender cambiform type, partially occluded as are the sieve tubes.

Gleditsia triacanthos

Mature. Sieve tubes short, with oblique end wall, with 4–10 narrow sieve plates; tubes full of mucilage or protoplasm; lattice not apparent.

Companion cells not discernible because of heavily staining sieve tube contents.

Parenchyma of elongate divided-cambiform type.

Robinia Pseudo-Acacia

Mature (figs. 30, 36). Sieve tubes of type 1, without lattice; sieve plates 35–40 μ in width.

Companion cells abundant in corners of sieve tubes.

Parenchyma of broad conducting type, thin-walled with abundant pitting.

Mature growing (figs. 31, 32). Formation of rows of parenchyma and of sieve tubes from cambium cells of same length. Otherwise no new features.

Mature root. Differs from mature stem only in having reduced amount of sclerenchyma.

Four-year stem. Sieve tubes of same type as mature but much smaller; small aggregations of slime near center of each; sieve plates poorly developed, 10–15 μ in width; lattice not apparent.

Companion cells present in most of the sieve tubes.

Parenchyma very abundant; heavily pitted on the radial walls.

Four-year root. Very similar to stem of same age but with more storage parenchyma and less sclerenchyma.

Two-year stem. Much as in four-year material, but fewer sieve tubes as compared with parenchyma; sieve tubes very small, with poorly developed plates 7–10 μ in width.

Parenchyma very abundant; packed with starch.

Two-year root (fig. 35). Like stem of same age but more storage tissue.

One-year stem, one-year root. Sieve tubes very small with poorly developed sieve plates; would not be recognizable except for dark-staining slime; very similar to parenchyma in size and shape.

Ailanthus glandulosa

Mature (fig. 29). Sieve tubes collapsed except close to cambium; large, very thin-walled, with usually a single transverse sieve plate; rarely 2–3 sieve plates. Pores of sieve plate very large; lattice not present.

Companion cells probably present but not observed on account of condition of material.

Parenchyma of conducting type; very thin-walled, in strands accompanying the sieve tubes; a second type of parenchyma with rounded ends forming loose tissue between sieve-tube groups.

Mature growing, mature root. Showed no different features.

Five-year stem. Sieve tubes small but with single transverse plate; pores in plate frequently few.

One- to two-year stem. Sieve tubes of type 3, the same as in mature; very rare.

Parenchyma of elongate cambiform type.

Rhus typhina

Mature. Phloem tissue uniformly thin-walled; sieve tubes abundant, with 1–5 sieve plates upon an oblique end wall; frequently only a single plate; lattice not well developed.

Companion cells abundant in corners of tubes.

Parenchyma of conducting type, very thin-walled; cells about the same size as the sieve tubes.

Three-year stem. Sieve tubes abundant but forming smaller proportion of phloem than in the mature; end walls either transverse or oblique with one plate or several; sieve plates rarely on side walls of tubes; lattice not seen.

Parenchyma the same as in mature.

Three-year root. The same as stem except for the presence of more storage tissue filled with starch.

One-year stem, one-year root. Essentially the same as in three-year material; fewer sieve tubes in proportion to parenchyma.

Acer saccharum

Mature. Sieve tubes with a single transverse sieve plate in the majority of cases, frequently with 2–3 plates; lattice weak, a faint network of cellulose thickenings upon the side wall; pores of lattice distinct under the oil immersion objective.

Companion cells not readily distinguished because of condition of material.

Parenchyma of divided-cambiform type in irregular tangential bands.

Tilia americana

Mature (fig. 39). Sieve tubes of type 2 with 2–10 sieve plates; rarely a single transverse plate; lattice well developed, much as in Populus.

Companion cells abundant in corners of sieve tubes.

Parenchyma of two types: one narrow, divided-cambiform type heavily pitted on radial wall; the other large, thin-walled cells of conducting type, but nearly empty or containing crystals; both types in tangential bands.

Three-year stem, three-year root. Sieve tubes in small groups between large fan-shaped rays; small, few, of same type as mature.

Parenchyma of two types as in mature.

One-year root. Sieve tubes not found; cambiform and storage parenchyma abundant.

Two-year twig. Sieve tubes about the same size and type as in three-year seedling; more numerous in twig.

Eleagnus angustifolia

Mature growing (fig. 20). Sieve tubes of type 3 with somewhat inclined sieve plates; lattice much as in Ulmus.

Companion cells very abundant in corners of sieve tubes.

Parenchyma of short, broad, divided-cambiform type; thin-walled.

Cornus paniculata

Mature root (figs. 37, 38). Sieve tubes small, slender; usually with a single transverse sieve plate; sometimes with 2–4 plates upon an oblique end wall; lattice a fine network enclosing pores much as in Acer.

Companion cells present but not abundant.

Parenchyma of divided-cambiform type with conspicuous sieve-like pitting on radial and terminal walls.

Nyssa sylvatica

Mature. Sieve tubes very long with oblique end walls; type 1 with 4–15 plates; plates in many cases present over entire radial wall where in contact with another sieve tube; frequently separated rather widely; lattice a very faint network with distinct pores in the meshes.

Companion cells present but not abundant.

Parenchyma scattered among sieve tubes; short divided-cambiform, full of protoplasm; abundant pitting on radial walls.

Twig. Sieve tubes present with transverse sieve plates for most part; very thin-walled, resembling parenchyma cells but with easily recognized sieve plates.

Parenchyma of very elongate, divided-cambiform type.

Fraxinus americana

Mature. Sieve tubes about the same shape as cambium cells; type 2 with 3–6 plates; pores large; thin-walled; lattice not well developed.

Companion cells abundant in corners of sieve tubes.

Parenchyma of broad, divided-cambiform type; abundant, scattered among sieve tubes; very heavily pitted on radial walls.

Two-year stem, two-year root, fast growth. Sieve tubes small, few, thin-walled, with single poorly developed transverse sieve plates; lattice not observed.

Parenchyma as in six-year stem.

One-year twig. Sieve tubes small, thin-walled, resemble parenchyma. Much like two-year seedling.

Fraxinus nigra

Mature. Sieve tubes of type 3, the single plate either transverse or somewhat oblique; pores in plate large; lattice a faintly developed network with fine pores.

Companion cells not observed on account of crushed condition of sieve tubes.

Parenchyma abundant; of divided-cambiform type, not very heavily pitted.

Cephalanthus occidentalis

Mature root (fig. 40). Sieve tubes long and narrow, with one or two round sieve plates either transverse or oblique; lattice not well developed.

Companion cells abundant.

Parenchyma, scattered cells of the conducting type, heavily pitted.

Sambucus canadensis

Mature (figs. 43, 44). Sieve tubes few, small, with oblique end walls, 10–20 plates; 20–30 μ in width, sometimes rather widely separated on the side walls; lattice not well developed.

Companion cells present in most of sieve tubes.

Parenchyma very abundant; short cambiform type, heavily pitted laterally.

Three-year root (fig. 42). Sieve tubes small and few, of same type as mature; plates 8–18 μ in width.

Parenchyma full of starch, as are all cells of xylem except vessels; not conspicuously pitted.

Sambucus racemosa

One-year stem (fig. 41). Sieve tubes small and scarce; 1–5 sieve plates on end wall.

Companion cells present.

From the foregoing descriptions of material it becomes evident that there are certain differences and certain similarities between the conditions found in the phloem of seedlings and in that of mature plants. Among the similarities, perhaps the most significant observation, from the standpoint of the present research, is that apparently there is no fundamental difference between the type of sieve tube found in seedlings and that found in the mature condition. Species having sieve tubes with transverse sieve plates in the mature plant show the same type in the seedling, *e. g.*, Robinia, Ailanthus, and Ulmus. In plants with sieve tubes of types 1 and 2, such as Populus, Juglans, Liriodendron, and Sambucus, the similarity between the sieve tubes of seedlings and adults is apparent, though not so marked, in that the seedlings of these plants show sieve tubes with a smaller number of sieve plates and frequently with a single transverse plate. Such a reduction in number of plates might perhaps be taken to indicate that the single transverse plate is the primitive condition. It seems more probable, however, that the small number of sieve plates in the sieve tubes of seedlings is due to the greatly reduced size of these elements in the young plants. If such is the case, the significance of the small number of sieve plates in the sieve tubes of seedlings of plants with the first and second types of sieve tubes in the adult, would be physiological rather than phylogenetic.

The extent of the differences in size between the sieve tubes of the seedling and those of the adult is readily shown by the following series of measurements of the radial width of sieve plates upon the end walls of sieve tube elements and by the series of photomicrographs.

Populus: one-year stem, fig. 4, 6–10 μ; three-year stem, fig. 5, 12–20 μ; four-year stem, fig. 6, 15–25 μ; mature, fig. 7, 30–45 μ.

Juglans: one-year stem, fig. 12, 8–12 μ; four-year stem, fig. 14, 6–18 μ; mature, fig. 15, 25–40 μ.

Robinia: two-year root, fig. 35, 7–10 μ; four-year root, 10–15 μ; mature, fig. 36, 35–40 μ.

Sambucus: three-year root, fig. 42, 8–18 μ; mature, fig. 43, 20–30 μ.

Since a single sieve plate extends completely across the sieve tube radially, its measurement may be taken as an accurate indication of the width of the tube. The difference in length between the sieve tubes in seedlings and those in mature plants is usually apparent also, but is not so marked. In fact, such difference in length is present in the cambium cells themselves, as is shown by figures 31 and 33 which are of like magnification. The first of these is taken from the tangential section of the cambium of a four-year seedling, whereas the second comes from a similar position in a mature stem.

These figures show that in passing from the one-year seedling to the adult, there is a gradual increase in the size of the sieve tube. Such small size as that indicated for the younger seedlings would make the presence of the adult number of sieve plates on the end wall impossible, without extreme reduction either of the size or of the number of pores upon the sieve plate. As a matter of fact, such reduction in size and number of pores does occur but not to the extent necessary for the accommodation of so large a number of plates on an end wall.

The small size of the sieve tubes in seedlings is correlated with the small number of these elements that are present in phloem of young plants, as compared with the number of parenchyma cells. This is graphically shown in Populus (figs. 4, 5, 6), Juglans (figs. 12–14), Robinia (fig. 35), and Sambucus (figs. 41, 42). It is further shown in the two figures of Robinia (34, 32), which are taken from tangential sections of the phloem near the cambium in a four-year seedling and a mature tree, respectively. Figure 34 shows that the cambium is developing almost entirely into parenchyma cells, whereas figure 32, representing the condition of a homologous portion of the phloem of the mature plant, shows the formation of an abundance of sieve tubes in addition to the parenchyma.

No seedlings were found in which the number of sieve tubes as compared with the number of parenchyma cells was not much smaller than in the mature plant. In fact, in some of the one-year seedlings this condition was so extreme that no sieve tubes could be found even after long search with the oil immersion lens (*e. g.*, Tilia and Robinia). This, of course, does not mean that sieve tubes are entirely absent, but it does at least indicate that they are very rare.

In many of the younger seedlings examined, as indicated throughout the description, the few sieve tubes that were found were poorly developed. The sieve tubes themselves were very small (see figs. 4, 5, 12, 35); the lattice was very faint or not discernible, and the sieve plates were frequently either without distinct pores or with very minute pores, and were not placed with any regularity upon the walls. In some cases the sieve tube elements were so much like parenchyma in size and shape that they could not easily be distinguished. For example, in the two-year seedlings of Robinia ready recognition of the sieve tubes would be impossible, were not red-staining slime strands present in these elements.

The phloem of the one-year-old twigs of mature plants shows many of the features found in seedlings, although they are not so extreme. Thus the first annual ring of phloem generally shows poorly developed sieve tubes without lattice and sometimes without well-developed sieve plates. The sieve tubes are fewer in number, as compared with the number of parenchyma cells, than in the adult, and a greater proportion of the sieve plates are transverse. The size of the sieve plates, also, is much smaller than in the mature plant, as shown in *Juglans nigra*. Here there is an increase in the size of sieve plates from 12–20 μ in the two-year twig to 25–40 μ in a twelve-year-old branch.

The structure of the phloem of seedlings as indicated in the foregoing observations, especially as regards the small number and poor development of the sieve tubes and the abundance of well-developed parenchyma, strongly suggests the possibility that in seedlings the conduction of protein material may take place, in large part, through the heavily pitted parenchyma. Of course it cannot be stated with certainty that such is the case, for it cannot be assumed that the few sieve tubes present in seedlings are not sufficient to supply the necessary conduction. Yet it seems reasonable to suppose that in a thrifty seedling considerable protein must be conducted through the phloem in excess of the apparent accommodation for such conduction through sieve tubes. It is well known that certain proteins may be conducted through parenchyma, as in the central cylinder of some of the mosses, the endings of the vascular bundles in leaves, and in the leptome parenchyma, discussed by Haberlandt (4, p. 329). The structure of seedling phloem suggests that such may be the case there also, and that the sieve tube, being a highly complex and specialized structure, is not well developed until later in the ontogeny of the plant.

In comparing the phloem of roots with that of stems, no essential differences are found in type of sieve tubes. This fact has been previously brought out by Russow (16, p. 205). The phloem of the root shows minor differences from that of the stem, in that in the latter there is usually a greater amount of sclerenchyma. In the material examined, the only exception to this condition is the root of *Viburnum Lentago*, where the masses of sclerenchyma in the root were considerably larger than those in the stem. Another point to be brought out is that the phloem of roots, particularly that of seedlings, shows a greater abundance of storage parenchyma differing from ordinary phloem parenchyma in that the cells are more nearly globose. In some seedlings practically all the phloem tissue is composed of cells of this sort. This condition may be so extreme as to give the impression that sieve tubes are fewer in number in seedling roots than in stems of the same age. Such seems to be the fact in a number of species, but as the observations lack the confirmation of actual count and measurement, it cannot be so stated with certainty.

The great variation in the type and distribution of sclerenchyma in phloem tissue, a condition of course comparatively well known, is clearly brought out in this study. All conditions may exist from a nearly complete absence of sclerenchyma, as in Maclura and Rhus, to practically solid masses of fibers and stone cells making up the entire older phloem of Fagus and Platanus. In the latter type all the phloem tissue, except that actually functioning, soon becomes converted into, or completely crushed by, sclerenchyma. Fibers may be scattered singly throughout the phloem as in Cephalanthus (fig. 40), arranged in regular tangential bands as in Salix and Tilia (fig. 39), or placed in irregular groups. They may be fairly straight, as is usually the case, or may be very much contorted and twisted as in *Acer rubrum*. Stone cells may occur singly or, as is more common, may be grouped in irregular masses. Both fibers and stone cells are frequently grouped together in various ways. The distribution of sclerenchyma is distinct for a given species, and within a species is fairly constant as far as the number of collections concerned in this study show.

The origin of fibers and stone cells in the phloem seems to be very different in different plants. In many cases fibers are cut off by the cambium in regular tangential bands and therefore appear near the cambium. Just as frequently, however, sclerenchyma is not present except in the outer phloëm, in which case it is formed either by the lignification of existing parenchyma cells formed by the cambium, the proliferation of parenchyma and its subsequent lignification, or possibly by the formation of rows of sclerenchyma by a layer of cells comparable to a phellogen layer. Frequently the medullary rays are lignified along with the masses of parenchyma through which they pass.

Crystals are of very frequent occurrence in the phloem of many plants. Probably the rhomboidal type is the most common, occurring abundantly within stone cells and septate fibers and also in different types of parenchyma. Druses are frequent but usually within parenchyma cells rather than sclerenchyma. The type and distribution of crystals, however, seems to vary with ecological conditions and rapidity of growth.

The parenchyma in the phloem of the mature woody plants studied is rather surprisingly uniform, the divided-cambiform type of Haberlandt (4) or modifications of it being of almost universal occurrence. The true cambiform type of cell with prosenchymatous form was not found in any of the plants studied, and the so-called conducting type was found in only a few, *e. g.*, Tilia and Cephalanthus. In fact, from the material studied, it seems practically impossible to make a good distinction between the cambiform and the conducting types because of the intergrading forms, a point brought out by Strasburger (17). In the development of secondary phloem parenchyma, an elongate cambium cell (figs. 10, 31) divides longitudinally to produce a parenchyma mother cell, which in turn divides transversely to form the parenchyma cells proper. This gives rise to a vertical series of cells with the cell at each end of the series pointed, as was the cambium from which it was formed (figs. 11, 32). Parenchyma of the true cambiform type would be produced either by the failure of the parenchyma mother cell to divide transversely or through its division by oblique cross walls so that resulting cells would be prosenchymatous in shape. Such division, however, was not observed, the cross walls being nearly transverse in all cases. The divided-cambiform type shows great variation in shape and size, from elongate, narrow cells with little radial depth, to nearly cubical cells approaching the conducting type.

The pitting in the divided-cambiform parenchyma is in most cases very prominent on the radial and terminal walls. Frequently the pits are grouped so as to present a sieve-like appearance as shown in the parenchyma of *Cornus paniculata* (figs. 37, 38), *Castanea dentata*, and others. In some species the pitting is not so pronounced, but the entire walls of the cell are thin and probably allow rapid diffusion. These types of parenchyma, according to Haberlandt (4), serve in the conduction of carbohydrates and the more easily diffusible proteins, a function for which they are apparently well suited histologically.

As before indicated, the present study does not confirm the phylogenetic significance of sieve-tube type as maintained by Hemenway (6). In making such a statement, of course, it must be borne in mind that in evolutionary development morphological characters do not advance equally. A given group may thus have one character highly developed and yet possess others remaining at a low level, as, for example, the presence of the inferior ovary, a "high" character, in "low" families such as the Juglandaceae and the Hydrocharitaceae. It must be recognized, also, that the number of species in this research is perhaps too small, as compared with the vast number of woody plants in the world flora, to justify the making of any sweeping generalizations. It is particularly unfortunate, too, that there are not included representatives of the tropical floras where woody plants form so large a proportion of the whole. Yet, inasmuch as the material examined was selected to represent, in so far as possible, a series of woody plants from the lowest to the highest forms in the Engler system, and since references in literature to the phloem of tropical woody plants show that the condition found there is not different from that in the northern flora, it seems not unreasonable to suppose that the facts revealed in this research give at least a fairly accurate indication of the conditions present in woody plants as a whole.

In view of the facts brought out in this study and confirmed in literature, it cannot be said that there is definite evidence of gradual advance in the evolution of the sieve tube from type 1 to type 3; at least, if there is such an advance it does not in any way parallel our present ideas of phylogeny. Indeed, Hemenway does not appear to be justified in making his types for sieve-tube classification as indicated by his figures (shown earlier in this paper), because in that classification the oblique end wall with many sieve plates is correlated with well-developed lattice, or sieve plates upon the side walls and the transverse end wall bearing a single plate with poorly developed lattice. From the description of material it is evident that no such correlation exists. For example, both *Ulmus americana* (fig. 17) and *Eleagnus angustifolia* (fig. 20) have single transverse sieve plates, and at the same time well-developed lattice. A similar condition was also pointed out in *Fagus sylvatica* by Dippel (3, p. 255), and later for *Ficus elastica* by De Bary (2, p. 177). Cases where the end walls are oblique and the lattice not well developed are even more numerous, *e. g.*, *Nyssa sylvatica*, *Alnus incana*, *Catalpa bignonioides*, *Fraxinus americana*, and others. Here the end walls are very oblique with from four to fifteen plates, whereas the lateral sieve fields are not clearly differentiated, the side walls being almost without cellulose thickenings and closely set with pores.

Table 1 shows in a graphic way that the sieve tube does not undergo a transition from type 1 to type 3 throughout the series of families as they are now placed in the evolutionary scale. It represents a partial list of the genera examined, arranged in phylogenetic order. Sieve tubes are classified according to the number of sieve plates on the end walls without reference to the side walls. As previously stated, number 1 indicates the lowest type with many sieve plates upon the end wall and number 3 the highest type with a single transverse plate. It is, of course, understood that such a definite classification cannot be actually made since all manner of intergrading forms exist. Under vessel types the scalariform, or lowest, is referred to by number 1, the porous, or highest, by number 3, and those forms which have both scalariform and porous vessels by number 2. Under parenchyma distribution the lowest, or terminal, position is indicated by number 1,

TABLE 1

	Sieve Tube Type	Vessel Type	Wood Parenchyma Distribution
Salicaceae			
Populus deltoides	1	3	1*
Salix nigra	1	3	3
Juglandaceae			
Juglans cinerea	1	3	2
Carya cordiformis	1	3	2
Betulaceae			
Ostrya virginiana	1	3	2
Betula lutea	2	1	2
Alnus incana	1	1	2
Fagaceae			
Fagus grandifolia	3	3	2
Castanea dentata	2	3	2
Quercus alba	2	3	2
Urticaceae			
Ulmus americana	3	3	3
Celtis occidentalis	3	3	3
Maclura pomifera	3	3	3
Morus alba	3	3	3
Magnoliaceae			
Magnolia acuminata	2	2	1*
Liriodendron Tulipifera	2	1	1*
Lauraceae			
Sassafras variifolium	3	2	3
Benzoin aestivale	3	3	3
Platanaceae			
Platanus occidentalis	2	2	2
Rosaceae			
Pyrus Malus	1	3	2
Prunus serotina	2	3	2
Prunus Persica	3	3	2
Leguminosae			
Gleditsia triacanthos	2	3	3
Robinia Pseudo-Acacia	3	3	3
Simarubaceae			
Ailanthus glandulosa	3	3	3
Anacardiaceae			
Rhus typhina	2–3	3	3
Aceraceae			
Acer saccharum	2–3	3	3
Acer Negundo	2–3	3	3
Sapindaceae			
Aesculus Hippocastanum	2	3	3
Tiliaceae			
Tilia americana	2	3	2
Eleagnaceae			
Eleagnus augustifolia	3	3	2
Cornaceae			
Cornus paniculata	2–3	1	2
Nyssa sylvatica	1	1	2

* In the starred species the position of the parenchyma is thought to be reduced condition rather than a truly primitive one (9).

TABLE 1—*Continued*

	Sieve Tube Type	Vessel Type	Wood Parenchyma Distribution
Oleaceae			
Fraxinus americana	2	3	3
Fraxinus nigra	3	3	3
Bignoniaceae			
Catalpa bignonioides	2	3	3
Rubiaceae			
Cephalanthus occidentalis	2–3	3	2
Caprifoliaceae			
Viburnum Lentago	1	1	2
Sambucus canadensis	1	2	1

the diffuse, or intermediate, position by number 2, and the highest, or vasicentric, position by number 3.

It will be noted in table 1 that there is considerable discrepancy between the classification of material in this study and that given by Hemenway. That author, as before stated, places all the woody dicotyledons in the two lower types and lists seventy-five genera of woody plants, according to sieve-tube type, almost exactly in phylogenetic order. That such an arrangement is not true to fact is shown beyond question by the present research, and further, is amply confirmed by an examination of literature. Of the species of woody plants placed in types 1 and 2 by Hemenway, the following species were found to have sieve tubes distinctly of type 3, the highest type; *Fagus grandifolia, Ulmus americana, Celtis occidentalis, Maclura pomifera, Morus alba, Sassafras variifolium, Robinia Pseudo-Acacia,* and *Ailanthus glandulosa.* The transverse nature of the sieve plates of Ulmus, Maclura, Morus, Robinia, and Ailanthus is shown in figs. 16, 18, 19, 30, and 29 respectively. Further confirmation of the above-cited determinations is given in the case of Fagus and Maclura by De Bary (2), Ulmus, Morus, and Ailanthus by Lecomte (13), and Robinia by Strasburger (17).

An idea of the extent to which the transverse sieve plates are found in woody plants is shown in the list given in table 2, compiled from Russow (16), Lecomte (13), De Bary (2), Janczewski (10), and Strasburger (17). The names are arranged in phylogenetic order and each is followed by the initial of the author referring to it.[4]

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[4] These same authors also make frequent reference to woody plants having sieve tubes with oblique end walls. As this is recognized to be a common type, however, a compiled list has been omitted to economize space.

Table 2

- Piperaceae
  - Piper Cubeba (R.)
- Fagaceae
  - Fagus sylvatica (D.J.)
- Ulmaceae
  - Ulmus effusa (L.)
  - U. montana (R.)
- Moraceae (L.)
  - Maclura (D.)
  - Ficus macrophylla (R.)
  - F. stipulacea (R.)
  - F. carica (R.D.)
- Artocarpaceae (L.)
- Berberidaceae (L.)
- Anonaceae
  - Anona Chierimolia (R.)
- Ranunculaceae
  - Atragene (R.)
- Rosaceae
  - Spiraea (L.)
  - Rosa (L.R.J.)
  - Amygdaleae (L.)
- Leguminosae
  - "Papilionaceae" (L.) (R.)
  - Cytisus (R.)
  - Robinia (S.)
  - Halimodendron (R.)
- Simarubaceae
  - Ailanthus glandulosa (L.)
- Malpighiaceae (L.)
- Buxaceae
  - Buxus (L.)
- Coriariaceae
  - Coriaria (R.)
- Anacardiaceae
  - Pistacia (L.)
- Aquifoliaceae
  - Ilex aquifolium (R.)
- Rhamnaceae (L.)
- Vitaceae
  - Vitis canescens (L.)
- Sterculiaceae (L.)
- Cornaceae (L.)
- Oleaceae
  - Fraxinus excelsior (R.)
- Asclepiadaceae
  - Asclepias (L.)
- Verbenaceae (L.)

It is readily seen by a study of tables 1 and 2 that transverse sieve plates are present in many genera of woody dicotyledons without reference to their phylogenetic position. Not only is there no gradual transition in type from the lowest to the highest, but further, in many families and even in some genera the type of sieve tube is not constant. High and low types of sieve tubes follow each other without any apparent correlation. Thus in Fagus and the Urticaceae, where low types might be expected, we find the single transverse sieve plate to be of universal occurrence, whereas in the Caprifoliaceae the sieve tube is definitely of type 1.

Variation in sieve-tube type within families is in some cases very striking. For example, in the Fagaceae the genus Fagus stands out as belonging to type 3, among genera of lower type. In the Cornaceae, the genus Nyssa has sieve tubes of type 1, whereas Cornus has sieve tubes almost entirely of the third type.

The woody Rosaceae and Leguminosae are additional examples. In the former, *Pyrus Malus* and *Prunus serotina* show sieve tubes of types 1 and 2 respectively, whereas *Prunus Persica* has sieve tubes of type 3 with few exceptions (fig. 28). In the tribe Caesalpinoideae of the Leguminosae type 2 prevails in *Gleditsia triacanthos* and *Gymnocladus dioica*, but in the tribe Papilionoideae type 3 is the rule, as shown in *Robinia Pseudo-Acacia* (fig. 30) and indicated in literature for Cytisus and Halimodendron (16).

In contrast with the families that show striking variation of sieve-tube type there are also those which show unusual uniformity. Thus the Salicaceae, Juglandaceae, and Betulaceae show almost universally the presence of sieve tubes of type 1, as shown both in the present research and in literature. The Urticaceae also, as indicated in tables 1 and 2, show the third type of sieve tube as a constant character. If sieve-tube type has any phylogenetic significance, it might well be argued that this family belongs higher in the scale of evolution than it now stands.

Sieve-tube type within the genus seems to be constant in the great majority of cases. Certain exceptions do occur, however, even in the rather small number of plants that have been examined. Perhaps the most glowing example of variation within a genus is shown in Fraxinus. Here *Fraxinus americana* has, beyond question, sieve tubes with oblique end walls as in Tilia, but *Fraxinus nigra*, as shown in this study, and *Fraxinus excelsior*, as shown by Russow (16), have sieve tubes with transverse end walls. In the genus Prunus, *Prunus serotina* has sieve tubes of the second type but *Prunus Persica* has those of type 3. This latter case is perhaps not so much to be wondered at because the two species are not closely related within the genus. An indication of this condition is shown in literature by Lecomte (13), who lists *Vitis canescens* as belonging to type 3, when it is well known that the "vine type" of phloem, as in *V. vinifera*, *V. labrusca*, and *V. vulpina*, has the oblique end wall. So far as has been determined, sieve-tube type is constant within a species. In the present study several collections of a species have been made in many cases, the material being chosen from different individuals and from various habitats, and in no instance has any essential discrepancy been apparent.

In view of the evidence brought out in tables 1 and 2, there seems to be no basis for the statement of Hemenway (6) that the study of the sieve tube adds further evidence to the theory that herbaceous plants are more advanced in evolutionary development than is the woody type. This theory regarding the position of herbaceous plants is doubtless well grounded; the point emphasized here, however, is that the so-called "herbaceous type" of sieve tube is of such common occurrence among woody plants that on the basis of our present knowledge there seems to be little foundation for the statement that the study of the sieve tube either adds to, or subtracts from, the evidence that herbaceous plants are highly advanced in the evolutionary scale.

Another statement by the last-mentioned author (6), which is not confirmed by the present research, is to the effect that companion cells are very rare, if not wanting, in many of the lower woody dicotyledons. It is, of course, realized that the companion cell is often difficult of certain recognition, even in the best preparations. However, if small nucleated cells containing neither starch nor "tannin" are present in the corners or along the sides of the sieve tubes, giving the appearance of having been cut off from the sieve tubes by division, it seems reasonable to conclude that such cells are companion cells. Cells of this type were found in fair numbers in all the material studied except in a few species in which the sieve tubes were so badly crushed that companion cells could not be recognized with certainty The presence of companion cells in woody plants belonging to the lower families is shown quite plainly in the photomicrographs of the transverse sections of *Populus deltoides* (fig. 7), *Juglans nigra* (fig. 13), and *Liriodendron Tulipifera* (fig. 22). Further, the presence of companion cells in Salix and Populus is described by Strasburger (17, pp. 211, 214), who also states that in Salix the companion cell may extend across the entire radial width of the sieve tube. It is evident, however, that these cells do not occur in the lower woody dicotyledons in such abundance as in the more highly placed families, as shown in *Tilia americana* (fig. 39), *Cephalanthus occidentalis* (fig. 40), and *Sambucus canadensis* (fig. 43).

On looking for correlation of sieve-tube type with type of vessel and wood parenchyma distribution, as indicated in table 2, it becomes evident that from the study of so small a number of species no marked relationships can be said to exist. For example, in the lower Amentiferae the lowest type of sieve tube is present in the same plants with the porous vessel and, in the case of *Salix nigra,* with the vasicentric type of parenchyma. In the genus Pyrus, also, sieve tubes of type 1 are associated with porous vessels and diffuse parenchyma. Examples of the association of the high type of sieve tube with the scalariform type of vessel are not so numerous, *Cornus paniculata* being the only good example noted.

In fact, although correlation between these structures does not stand out, it may be said that a fair percentage of cases shows sieve tubes, vessels, and parenchyma of approximately the same level of development according to types made. The large number of cases where no correlation exists is perhaps within the limits to be expected for morphological characters. It can also be said that the distribution of sieve-tube type in the phylogenetic sequence is apparently just as consistent with the idea that type 1 is primitive and type 3 advanced, as is the distribution of vessel type with the more widely accepted theory that the scalariform vessel is primitive, and the porous advanced; and if the types of vessel are given phylogenetic significance, sieve-tube types may also be given equal value. It cannot be stated, however, that there is a gradual advance in type of sieve tube without great variation or many exceptions in ascending the phylogenetic tree, as indicated by Hemenway (6).

The above-named author also appears to be unjustified in the statement that the sieve tubes of the Juglandaceae are like those of the gymnosperms and vascular cryptogams (5). The reason given for such an assertion is that the sieve tubes of the Juglandaceae have well-developed sieve plates upon the side walls which do not differ in structure and appearance from those upon the end walls, a condition similar to that present in the above-mentioned groups. In a later paper (6) it is stated that thirty species of the lower woody dicotyledons show the same sieve-tube structure as that found in the Juglandaceae.

These statements regarding the sieve tubes of the Juglandaceae and the "thirty species of lower dicotyledonous trees" are confirmed neither by the present research nor by literature. In the first place, as stated by Hill (7), the sieve plates of the gymnosperms, as illustrated by Pinus, have multiperforate sieve fields between the meshes of the cellulose framework, whereas in the angiosperms, as illustrated by Cucurbita, Wisteria, Vitis, and others, the sieve fields between the meshes of the sieve are perforated by a single large pore which takes up nearly the whole width of the mesh. In the present research, examination of the sieve plates and the lattice of the sieve tubes of Juglans, Salix, Populus, and others under high magnification, shows that there is such a discrepancy in the size of the pores on the lateral and terminal wall that they cannot be said to have the same structure. In all cases the pores on the sieve plates of the end walls are large enough to permit accurate measurement, but on the side walls the pores, though distinct, are so minute as to prevent such measurement even under the oil immersion. This condition is well brought out in the photomicrographs of *Populus deltoides* (figs. 2, 3). In fig. 2 the pores in the sieve plate on the end wall are plainly visible, but on the side wall the pores are so minute that they could not be recorded by the camera, being mere crowded points of light even under high magnification. The sieve plates and lattice of the Salicaceae studied are of nearly identical type with those found in the Juglandaceae. The difference in the size of the pores in the sieve plates and in the lattice is further shown by the measurements given in table 3.

TABLE 3

Juglans nigra	1.8–3.5 microns	.5–.6 micron
Populus deltoides	3.5–5.5 "	.5–.6 "
Salix nigra	2–3 "	.4–.5 "

If similarity to the gymnosperm type of sieve tube is found anywhere in the angiosperms, it apparently is not in the Juglandaceae but rather in such genera as Pyrus and Sambucus, which do show sieve plates of like structure upon both the side and end walls (figs. 26, 27, 44).

In conclusion, it may be said that the present research is not thought to refute the idea that sieve-tube type and type of vessel have phylogenetic significance. Either to confirm or to disprove those theories would require the examination of a vastly greater number of genera representing the floras of the world. Rather is it desired forcibly to bring out the fact that the evolutionary significance of any character is often obscure and that sweeping generalizations cannot be made upon the examination of a limited amount of material, even though the observations may be accurate. That histological and anatomical characters will have a very important influence upon the future ideas of phylogeny cannot be doubted. In the case of most characters, however, it remains for anatomical work on a scale much greater than that hitherto attempted to show what the real significance of those characters may be.

SUMMARY

The more important results of this study may be briefly stated as follows:

1. In the woody dicotyledons, there is no fundamental difference in type between the sieve tubes in the phloem of seedlings and those in the mature plant, existing differences being mainly those of size.

2. In the phloem of seedlings the number of sieve tubes as compared with the number of parenchyma cells is much smaller than in mature phloem.

3. Phloem of one-year-old twigs from mature trees has many of the characteristics found in the phloem of seedlings.

4. There is no gradual advance in sieve-tube type from type 1 to type 3 which parallels our present ideas of phylogeny.

5. All types of sieve tubes are present in the woody dicotyledons, the so-called "herbaceous type," with single transverse sieve plates, being probably about as frequent as any other.

6. Widely different types of sieve tubes are found in the woody species of the same family and sometimes even within the woody species of the same genus.

7. Companion cells are present in all families of the woody dicotyledons studied, although usually in smaller numbers than in the phylogenetically higher forms.

8. The sieve tubes of the lower woody dicotyledons are fundamentally different from those of the gymnosperms and vascular cryptogams.

9. There is little correlation between type of vessel and type of sieve tube.

The writer wishes to acknowledge his indebtedness to Dr. A. J. Eames, of Cornell University, under whose direction the work was carried on, and to Professor I. W. Bailey, of the Bussey Institution, Harvard University, for assistance in the use of photographic apparatus at his laboratory.

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EXPLANATION OF PLATES XXIV–XXIX

The following abbreviations are used in labeling the figures: st = sieve tube, sp = sieve plate, l = lattice or lateral sieve field, cc = companion cell, p = parenchyma, c = cambium, f = fibers, m = medullary ray. All figures are photographs of phloem except when otherwise designated.

Pinus Strobus

FIG. 1. Radial section showing distribution of sieve plates upon the radial walls of the sieve tubes. × 250.

Populus deltoides

FIG. 2. End wall of sieve tube showing perforations in the sieve plates. × 450.

FIG. 3. Side wall of sieve tube showing the lattice. The pores between the scalariform bars are very minute as compared with those in the sieve plates on the end wall. × 450.

FIG. 4. Transverse section, one-year-old root showing the small size and number of sieve tubes as compared with the mature condition (fig. 7). × 100.

FIG. 5. Transverse section, three-year-old stem showing the same features as figure 4. × 100.

FIG. 6. Transverse section, four-year stem showing same features as figure 4. × 100.

Populus deltoides

FIG. 7. Transverse section, mature root. Note increase in size and number of sieve tubes in series (figs. 4–7). × 100.

Salix nigra

FIG. 8. Tangential section, mature root, showing end walls of sieve tubes with sieve plates in section. The phloem of Salix and that of Populus are practically identical. × 100.

Carya cordiformis

FIG. 9. Tangential section, mature stem, showing lattice in face view and sieve plates in section. × 100.

Juglans cinerea

FIG. 10. Resting cambium, mature plant, showing shape of cells in tangentia section. × 100.

FIG. 11. Tangential section taken in the phloem near the cambium showing division of cambium cells to form parenchyma and sieve tubes. The sieve-tube elements are of the same length as the cambium cells. × 100.

FIG. 12. Transverse section of one-year stem showing small sieve tubes and abundant parenchyma. × 100.

Juglans nigra

FIG. 13. Transverse section of two-year root showing increase in size and number of sieve tubes as compared with one-year material (fig. 12). × 100.

FIG. 14. Transverse section of four-year stem showing increase in size and number of sieve tubes as compared with two-year material (fig. 13). × 100.

Juglans nigra

FIG. 15. Transverse section of mature stem. Note series (figs. 12–15). × 100.

Ulmus americana

FIG. 16. Radial section showing transverse sieve plates with slime strings adhering to them. × 250.

FIG. 17. Tangential section showing sieve tube with transverse sieve plate and well-developed lattice. × 270.

Maclura pomifera

FIG. 18. Radial section of mature stem showing transverse sieve plates. × 250.

Morus alba

FIG. 19. Radial section showing transverse sieve plates. × 270.

Eleagnus angustifolia

FIG. 20. Tangential section showing single, transverse, or oblique sieve plates and lattice. × 250.

Liriodendron Tulipifera

FIG. 21. Mature stem, transverse section. Sieve tubes in lower part near cambium are partially occluded with callus. × 100.

FIG. 22. Mature root, transverse section. Note much smaller amount of sclerenchyma as compared with stem. × 100.

FIG. 23. Radial section showing large sieve plates in face view upon the end walls and smaller well-developed plates on the side walls. × 180.

FIG. 24. Radial section, mature root, showing variation in size of sieve plates upon end and side walls. × 200.

FIG. 25. Same, tangential section showing sieve plates in section and close ontact of sieve tubes, parenchyma, and medullary rays. × 125.

Pyrus Malus

FIG. 26. Radial section showing sieve plates upon radial walls of sieve tubes. × 450.

FIG. 27. Same, tangential section showing sieve plates in section. In this species there is apparently no differentiation of side and end walls. × 270.

Prunus Persica

FIG. 28. Mature stem, tangential section showing single transverse oblique sieve plates. × 450.

Ailanthus glandulosa

FIG. 29. Mature stem, transverse section showing single transverse sieve plates in face view. × 450.

Robinia Pseudo-Acacia

FIG. 30. Mature stem, radial section showing transverse sieve plates, slime globules and probable companion cells. × 270.

FIG. 31. Resting cambium of mature stem, tangential section. × 100.

FIG. 32. Tangential section of phloem near the cambium showing development of cambium cells into parenchyma and sieve tubes. × 100.

FIG. 33. Cambium of four-year stem, tangential section showing smaller size of cambium cells as compared with the mature (fig. 31). × 100.

FIG. 34. Phloem near cambium of four-year stem, tangential section. × 100.

FIG. 35. Transverse section, two-year root. Note small number and size of sieve tubes as compared with mature (fig. 36). × 270.

Robinia Pseudo-Acacia

FIG. 36. Mature growing stem, transverse section. × 270.

Cornus paniculata

FIG. 37. Transverse section showing sieve-like pitting in end walls of parenchyma. × 450.

FIG. 38. Radial section showing sieve-like pitting on radial walls. × 450.

Tilia americana

FIG. 39. Transverse section, mature stem. Note two types of parenchyma. × 100.

Cephalanthus occidentalis

FIG. 40. Transverse section, mature stem. × 100.

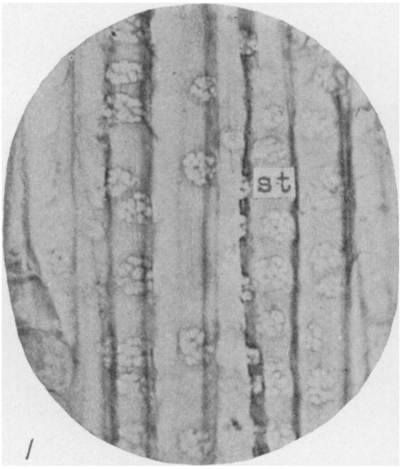
Sambucus canadensis

FIG. 41. Transverse section, one-year root. × 270.

FIG. 42. Transverse section, three-year root. × 270.

FIG. 43. Transverse section, mature stem. × 270.

FIG. 44. Tangential section showing sieve plates in section upon oblique end walls. × 270.



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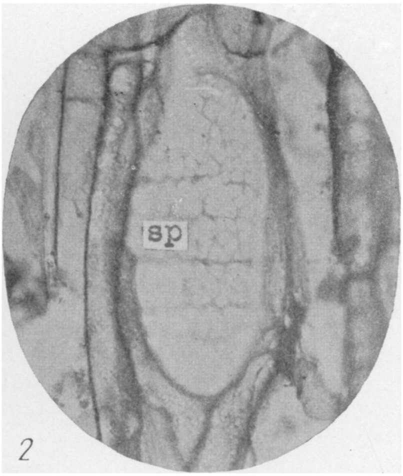

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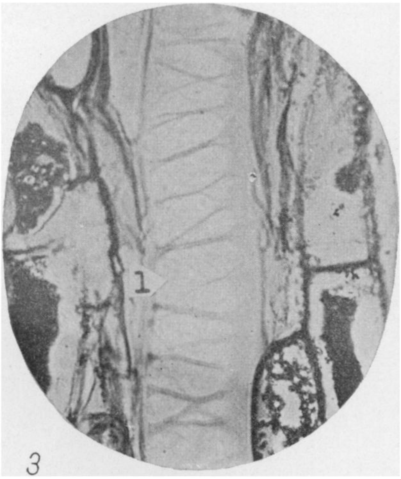

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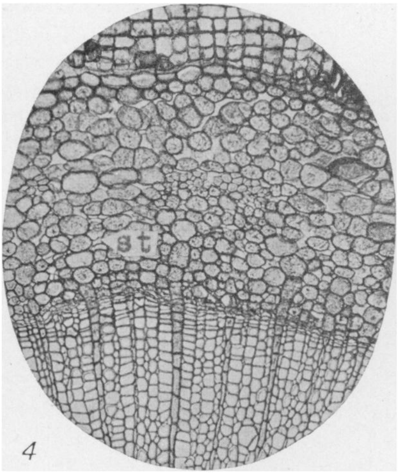

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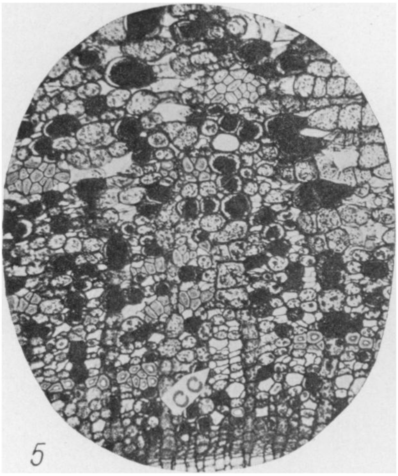

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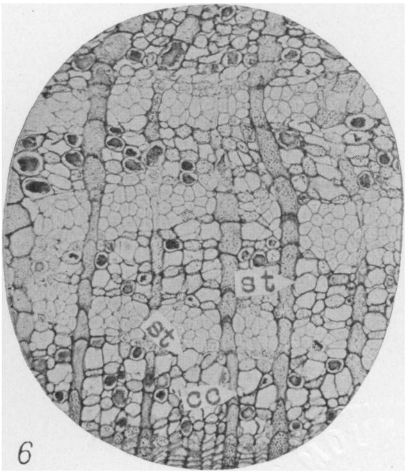

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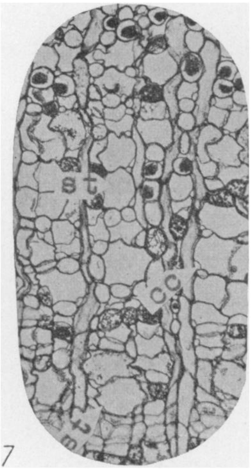

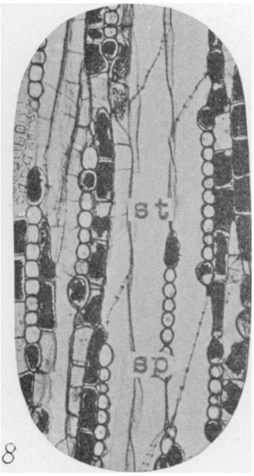

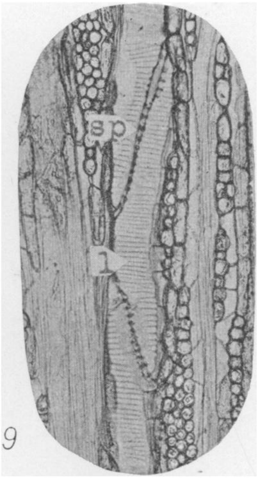

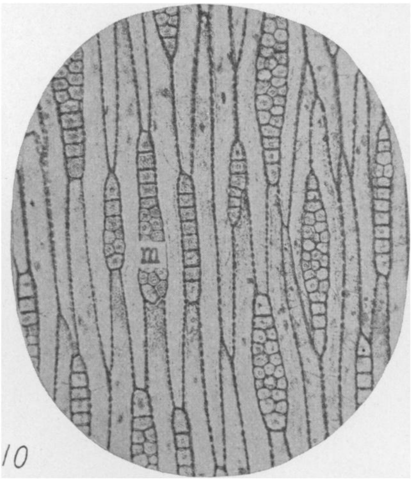

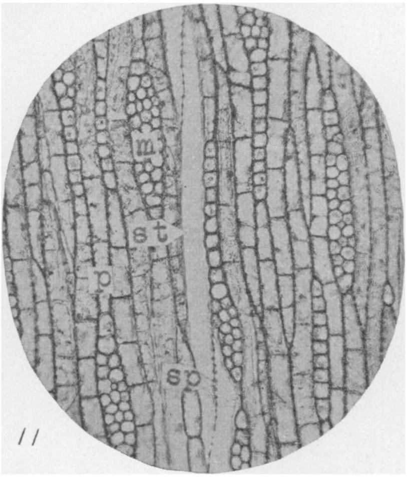

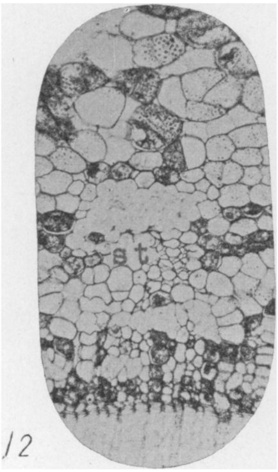

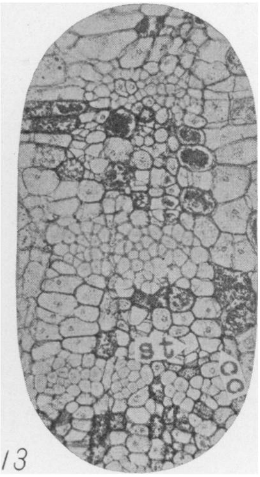

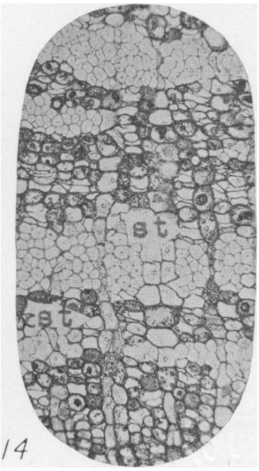

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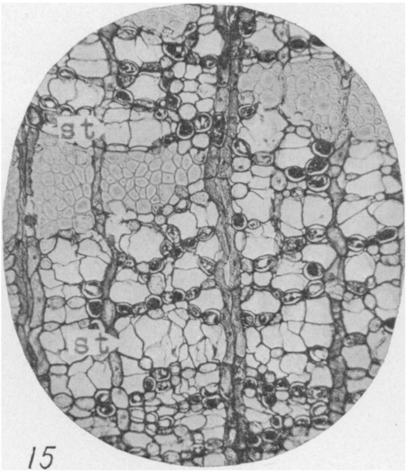
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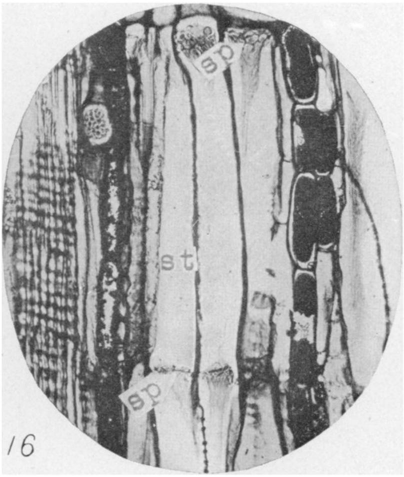
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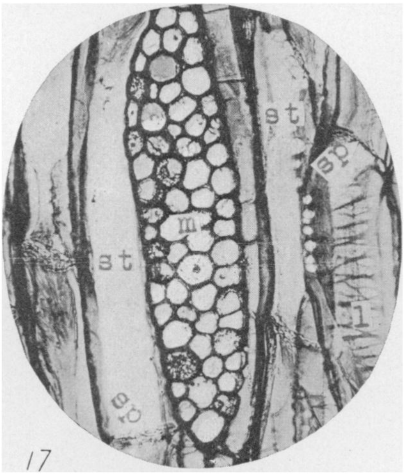
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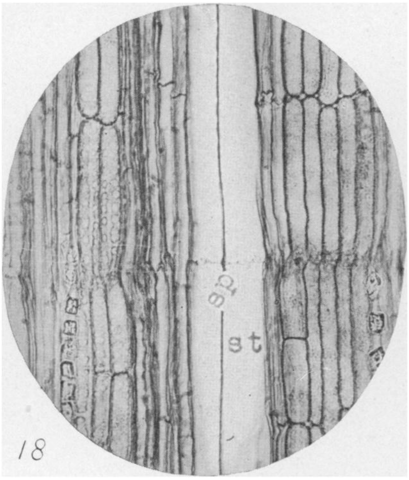
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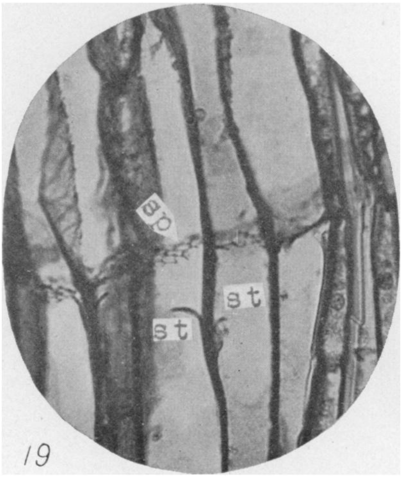
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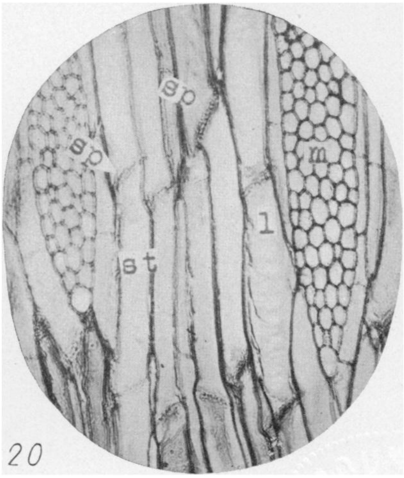
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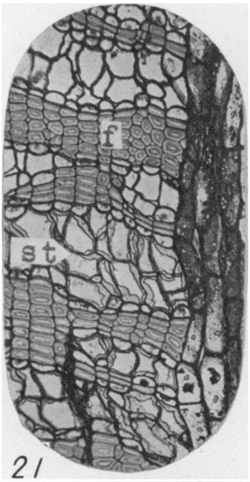

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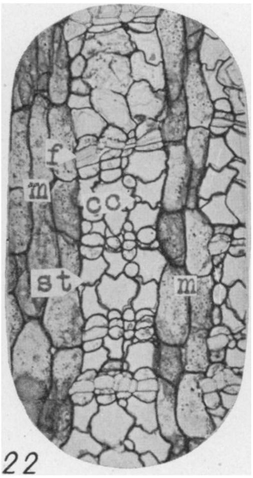

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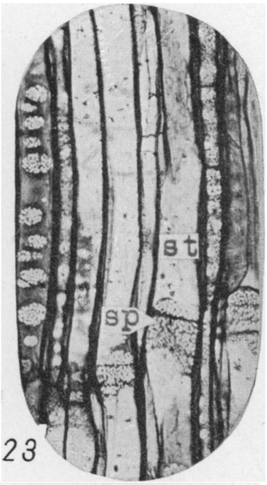

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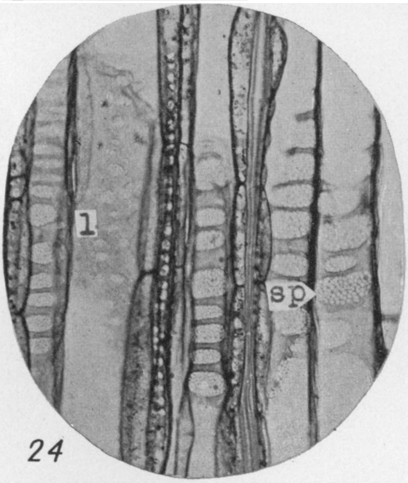

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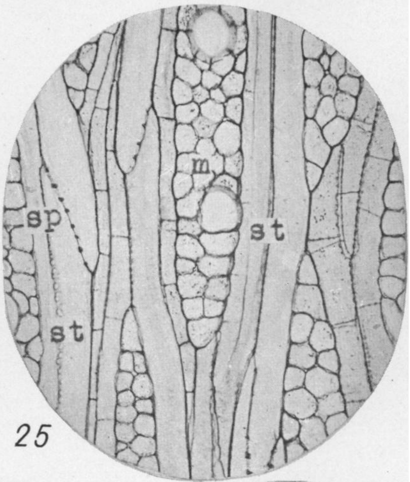

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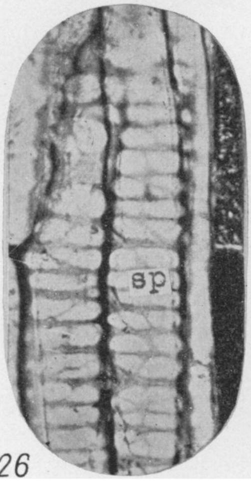

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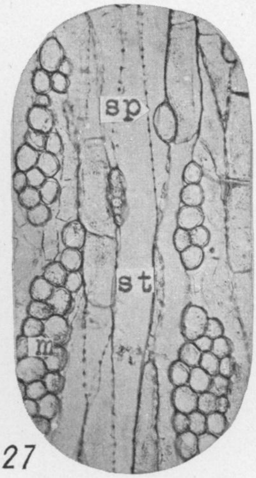

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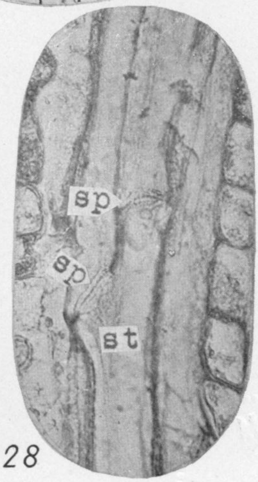

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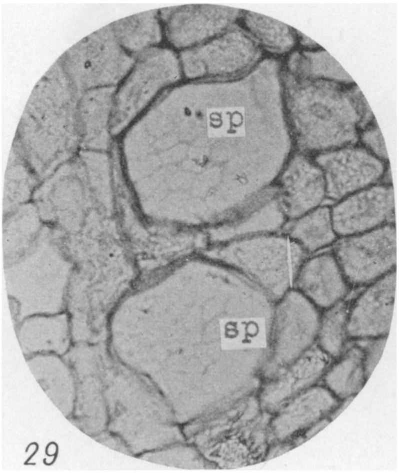
MacDaniels: Histology of the Phloem.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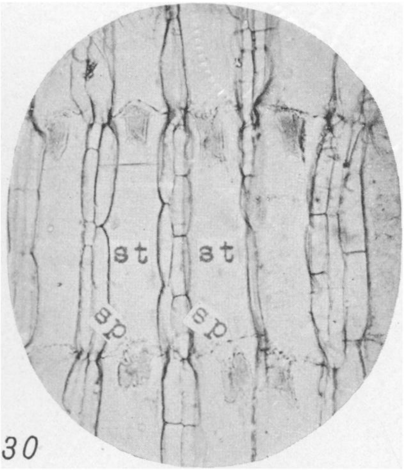
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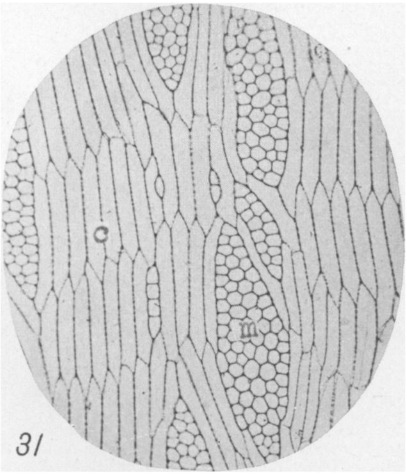
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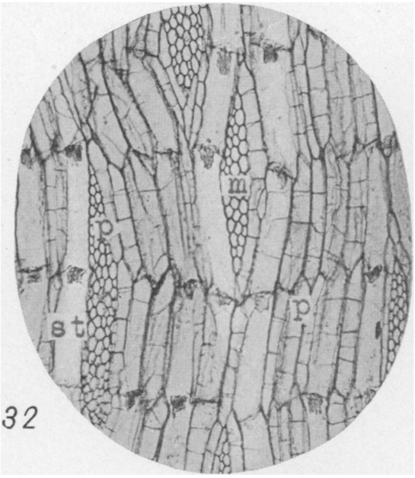
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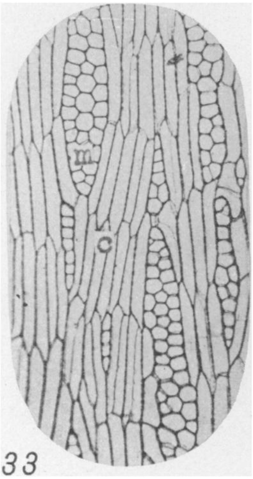
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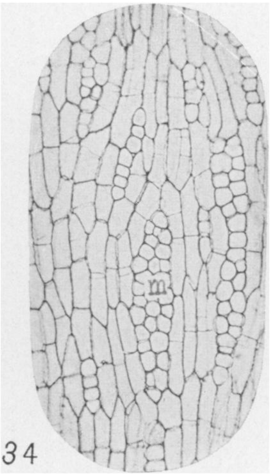
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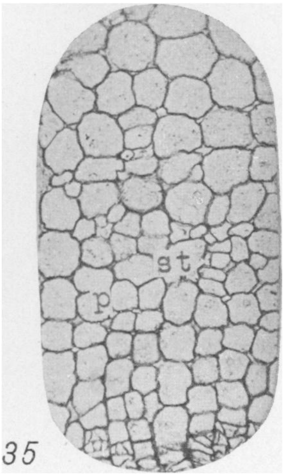
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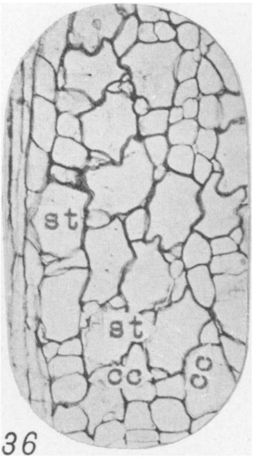
MACDANIELS: HISTOLOGY OF THE PHLOEM.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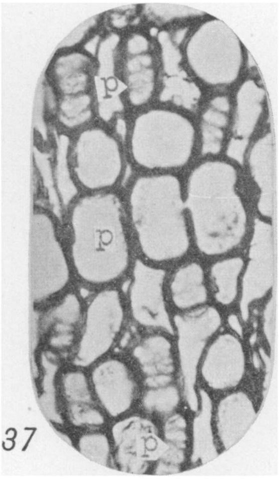
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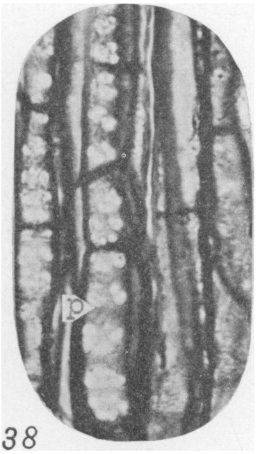
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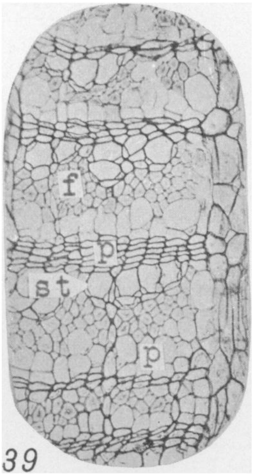
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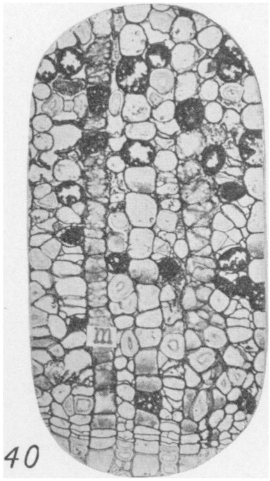
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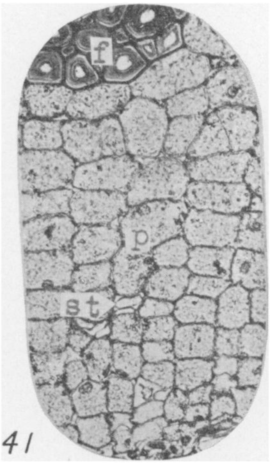
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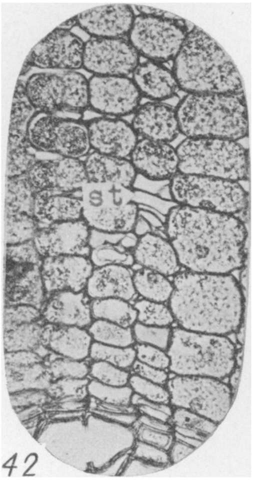
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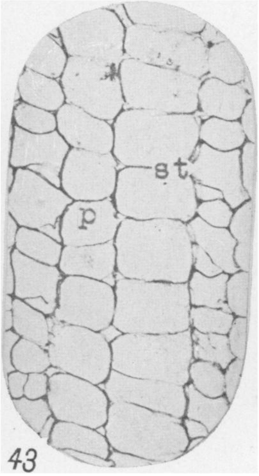
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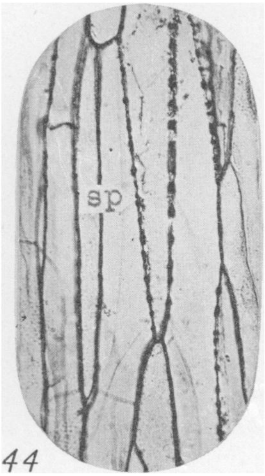
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